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CADMIUM EFFECTS ON HIGHER PLANTS

ABSTRACT: Cadmium (Cd) is a heavy metal widely distributed in the biosphere. Environmental pollution with Cd is widespread throughout the world. At higher concentrations, it is very toxic to living organisms. Plants absorb Cd from the soil solution rather easily, and it enters the food chain mostly through them. The availability of Cd for plants depends primarily on the chemical properties of the soil. During the uptake of Cd, interaction with ions of other elements may occur. Plant species differ in the intensity of absorption and thus accumulation of Cd, which is absorbed in the form of ions or chelates. Cadmium mostly accumulates in the roots and may then be transported by xylem and phloem. Toxic concentrations of Cd can cause a variety of unfavorable changes in the anatomical and morphological features of plants, affect physiological and biochemical processes, their mineral composition and reduce growth. Cadmium may inhibit germination by hindering water uptake and mobilization of seed reserves. The effect of Cd on photosynthesis was studied in the most detail. Higher concentrations of Cd adversely affect the synthesis of chloroplast pigments, photosynthetic electron transport and the Calvin cycle more than other processes. Some substances can be used to mitigate the phytotoxic effect of Cd, such as silicon, boron and biochar etc. Cadmium-hyperaccumulating plant species possess specific mechanisms by which they can mitigate the toxicity of higher Cd concentrations.

KEYWORDS: accumulation; heavy metal; Cadmium (Cd); distribution; growth; plants; photosynthesis; seed germination; toxicity

INTRODUCTION

Cadmium is a soft silver-white metal, belonging to the group of heavy metals (HM). Together with zinc and mercury, it is included in the II B group of the periodic table. Cadmium was discovered by Sreomeyer in 1817. The atomic

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number of Cd is 48, atomic weight is 112.41 g/mol. It is found in nature but in the form of salts. The most famous salt is $CdSO_4$ and it is also found in the form of CdS, $CdCl_2$ and $Cd(NO_3)_2$. In the air, it quickly turns into CdO. Heavy metals are among the biggest environmental pollutants (Karahan et al., 2020). They can pollute soil, air, water and plants. They are very toxic to all living organisms, microorganisms, plants, animals and humans. Cadmium can cause toxic effects in living organisms even at low concentrations. It is one of the most toxic heavy metals due to its high solubility in water and non-degradability. It can enter the human body primarily through ingestion and partly through the respiratory tract. It concentrates in bones, kidneys and liver, causing numerous serious diseases (Altio and Tritscher, 2004). Therefore, significant attention is paid to this element both from a health and ecological point of view. According to the World Health Organization (WHO), the weekly tolerable exposure to Cd is 0.007 mg/kg of body mass (WHO, 2000). Terrestrial plants mostly absorb Cd from the soil and the concentration of Cd in the Earth's crust is on average 0.15 to 0.20 mg/kg. The average concentration of Cd in the surface layer of soil, based on a large amount of data in different soil types and countries, ranges from 0.06 to 1.1 ppm in dry matter (Kabata-Pendias and Pendias, 2000). Numerous human activities lead to environmental pollution with Cd: mining and metal refining, municipal sewage sludge, animal manure, compost, mineral fertilizers, pesticides, atmospheric fall-out, coal fly ash, cement factories, natural mobilization of Cd by weathering of rocks and volcanic activity, etc. (Bogdanović et al., 1997; Kabbata-Pendias and Pandias, 2000; Rizwan et al., 2017). Cadmium is a harmful non-essential element for plants, humans and animals. Owing to its good solubility in water and high mobility in the soil, plants absorb Cd easily and more intensively compared to some other HMs. It can affect numerous physiological, biochemical and metabolic processes of plants. Owing to its chemical similarity with some other divalent cations (like Ca^{2+} and Mg^{2+}), Cd can substitute them in the active part of the molecule of some proteins and thus cause a disturbance in their function. The phytotoxicity of Cd is based, among other things, on its ability to bind to histidyl, thiol and carboxyl groups of enzymes and structural proteins, thus preventing their original physiological and biochemical action (Huybrechts et al., 2019). For the above and other reasons, excessive accumulation of Cd in plants can cause numerous morphological, physiological and biochemical disorders, the ultimate effect of which is reduced production of organic matter or even death. Cadmium-stress adversely affects photosynthesis and reduces chlorophyll content (Zhou et al., 2024), negatively affects seed germination (Chanpiwat and Numprasanthai, 2024), causes oxidative stress, production of superoxide free radicals resulting in DNA damage and lipid peroxidation of the cell membrane system (Hossain et al., 2012; Haider et al., 2021) and affects leaf structure and root anatomy (Kovačević et al., 1999; Maksimović et al., 2007). Considering the numerous environmental pollutants containing Cd and its toxicity at higher concentrations for living organisms, it is understandable that there is a great interest in this element.

Uptake, transfer and accumulation of cadmium

Plants can absorb Cd through the roots and leaves, stems and seeds. The sources of Cd can be soil, air and water habitats. The most significant is its absorption from the soil, where it is found in different forms, primarily in soluble and exchangeable form. Bioavailability of Cd depends on numerous chemical and physical properties of the soil, pH value, capacity of cation exchange, organic matter content, presence of ions of other elements, temperature, humidity and soil texture (Wei et al., 2023; Huang et al., 2021). The pH value of the soil is of particular importance for the bioavailability of Cd, since it decreases significantly in an alkaline environment. Acidic soils enhance Cd solubility, whereas liming immobilizes Cd. Soil organic matter binds Cd but can also form soluble complexes that increase mobility. Microbial activity modifies Cd bioavailability through siderophore production, root exudates, and mycorrhizal associations. Biochar and phosphate amendments have shown promise in reducing bioavailable Cd pools (Guan et al., 2025).

Cadmium enters roots via multiple transporter families: ZIP (ZRT/IRT-like proteins), NRAMPs, HMAs (heavy metal ATPases), and Ca^{2+} channels. The high-affinity Fe^{2+} transporter, IRT1, is a major Cd entry route in Arabidopsis (Tao et al., 2022). Once inside the root symplast, Cd is either bound by phytochelatins or exported into xylem vessels by HMA2/HMA4. Vacuolar sequestration is mediated by ABC transporters and HMA3. Transpiration stream largely drives Cd accumulation in leaves, whereas phloem mobility is relatively restricted, though grains of rice and wheat still accumulate Cd to toxic levels (Yu et al., 2024).

Due to the chemical similarity and charge characteristics between Cd and Ca, Fe(II), Zn and Mn, there is competition for their uptake and translocation in plants (McLaughlin et al., 2021). Cadmium toxicity affects N metabolism; the activity of some enzymes of N metabolism decreases, while the content of nitrates in plants increases (Kastori and Petrović, 1995). Optimal N supply decreases the stress induced by Cd in young sunflower (Panković et al., 2000). The Si alleviates uptake and accumulation of Cd in peanut and pea (Shi et al., 2010, Rahman et al., 2017). Reduction in rhizotoxicity and absorption of Cd by soybean and wheat roots were seen upon the application of Ca and K (Yang and Juang, 2015). Individual plant species and genotypes can differ significantly in intensity of uptake and accumulation of Cd (Petrović et al., 2003; Ai et al., 2022). Cadmium is absorbed by plants in the form of Cd^{2+} ions or in the form of chelating compounds. In the soil solution, Cd^{2+} ions reach the root surface by mass flow or diffusion. On the root surface, Cd adsorption occurs from the surface of rhizodermal cells through exchange with H^+ ions, after which Cd reaches the cortex through the apoplast (Sasaki et al., 2012). There is an opinion that the transport of Cd ions is carried out by the same transmembrane carriers that participate in the uptake of some other cations. After entering the root hairs, Cd is transported through symplast and apoplast pathways to the xylem (Shaari et al., 2024). In long-distance transport, xylem plays a key role. The driving forces of xylem transport are transpiration and root pressure. Phloem transport plays an important role in the redistribution of Cd in aerial organs (Tanaka et al., 2007). In general, it can be said that Cd is well mobile in plants, where transporter proteins play an important role (Hao et al., 2022; Zhang et al., 2024). Cadmium can also enter cells through the plasma membrane via Ca channels (Perfus-Barbeoch et al., 2002). Most of the absorbed Cd is retained in the roots, which can be considered as one of the protective mechanisms of above-ground organs against the toxic effects of Cd. In the case of beans, from the total Cd taken up, only 2% is transported to the aerial part. In the root, it is predominantly found in the apoplast or vacuole (Ouariti et al., 1997). In some plants, the cell wall plays a pivotal role in the accumulation of Cd (Peng et al., 2017). The presence of Cd in human and animal food is unacceptable; therefore, special attention is paid to the distribution of Cd in consumable parts of plants. The intensity of Cd accumulation in plants primarily depends on its concentration in the nutrient medium and it rises with its presence. (Logan et al., 1997; Dias et al., 2012). Cadmium also affects the accumulation of some micro- and macronutrients in plants. According to Dias et al. (2012), in the roots of young *Lactuca sativa* plants, Mn uptake was significantly decreased at 10 and 50 μM Cd, while in the leaves, Fe uptake significantly decreased. Plant species differ significantly in Cd accumulation. In soil enriched with 10 ppm Cd by sewage sludge, the concentration of Cd in the above-ground part among the 19 examined species, primarily cultivated, was the lowest in rice and the highest in turnip, 162.0 μg/g of dry matter. Significant differences between wheat genotypes in their response to different Cd concentrations were found *in vitro* (Kondić-Špika et al., 2005). Wheat cultivars originating from different parts of the world and then grown in the same ecological conditions differed only slightly in the accumulation of Cd in the grain. The concentration of Cd in the grain in the eight tested wheat genotypes was much higher in humid years (0.0423 mg/kg of dry weight) and was significantly lower in dry years (0.020 mg/kg) from the allowed maximum concentration (0.5 mg/kg) (0.3 mg/kg) (Maksimović et al., 2016). The World Health Organization (WHO) does not provide one single maximum permissible concentration (MPC) for cadmium in all plants (Commission Regulation (EU) 2023/915 of 25 April 2023). Worls Health Organization (WHO) and Food and Agriculture Organization (FAO) guideline suggests a maximum level of 0.2 mg/kg for leafy vegetables. However, other sources indicate different maximums, and some national limits are even higher for specific vegetables. For root vegetables, other organizations have set a maximum level of 0.3 mg/kg; for medicinal plants WHO have set a limit of 10 ppm (10 mg/kg); for rice, the allowable limit is often set at 0.2 or 0.4 mg/kg. There are plant species that are characterized by higher accumulation of Cd, so-called hyperaccumulators, such as bermuda grass, vetiver grass, bulrush, and turnip. They are characterized by a higher bioconcentration and translocation factor for Cd (Shanying et al., 2017). Owing to that, some of them can be used for phytoremediation of Cd-contaminated soils.

Effects of cadmium on seed germination

Seed germination is one of the most important events in the life cycle of plants. It can be influenced by numerous exogenous and endogenous factors, including the presence of Cd (Carvalho et al., 2023; Jabri et al., 2024; Chanpiwat and Numprasanthal, 2024). The first step towards germination is absorption of water, since it is essential for activation of hydrolytic enzymes and for hydrolysis of organic compounds stored in the endosperm. This initiates metabolic processes, including respiration and various anabolic pathways necessary for the growth and development of the embryo. Higher concentrations of Cd can weaken water absorption and thus limit the availability of water for the development of embryos and seedlings (Kuriakose and Prasad, 2008). The absorption of water depends on the structure of the seed coat as well as on the presence of osmotically active substances in the seed. Their presence, however, depends on the activity of hydrolytic enzymes, which is affected by Cd. Kalai et al. (2016) reported a reduction of alpha-amylase activity in germinating barley seed influenced by Cd stress, resulting in a decrease in starch release from cotyledons. A decrease in the activity of hydrolytic enzymes such as alpha-amylase, acid phosphatase and proteases in *Sorghum bicolor* led to a decrease in the mobilization of the seed nutrient reserves (Kuriakose and Prasad, 2008). Cadmium can affect the production of reactive oxygen species (ROS) and tangle the antioxidant system, which can affect numerous processes in plants, including seed germination (Senevirante et al., 2019). Elevated ROS (O_2^-, H_2O_2, HO•) causes lipid peroxidation (e.g., increased MDA), protein oxidation and DNA damage. Cadmium does not directly generate reactive oxygen species (ROS), but it interferes with electron transport chains in chloroplasts and mitochondria, leading to ROS overproduction. Reactive Oxygen Species (ROS) such as H_2O_2 and O_2 – cause lipid peroxidation, protein oxidation, and DNA damage. Plants respond with enzymatic antioxidants (SOD, CAT, APX, GR) and non-enzymatic antioxidants (ascorbate, glutathione, flavonoids). The balance between ROS production and scavenging capacity determines tolerance (Seregin & Kozhenkov, 2023).

According to Han et al. (2023), the antioxidant enzymes of wheat seeds and seedlings decreased under Cd pollution. Cadmium also affects phytohormones, which play a significant role in the processes of decomposition of organic matter accumulated in the endosperm during seed germination (Huybrechts et al., 2019). Seeds intensively absorb Cd dissolved in water, especially at higher concentrations. Higher concentrations of Cd adversely affect germination, seedling vigor and increase the percentage of atypical seedlings (Kastori et al., 2019). Based on a large number of literature data, Senevirante et al. (2019), and Carvalho et al. (2023) state that Cd does not always have a negative effect on germination and seedling vigor, but may have a neutral or even positive effect depending on the dose of Cd, properties of the medium, plant species and genotype, the state of plant and organ development.

Effect of cadmium on photosynthesis

Photosynthesis is of vital importance for higher plants, since in this process, organic matter is synthesized from CO_2 and water, using solar energy. Therefore, numerous researchers have recently studied the influence of Cd on photosynthesis (Chu et al., 2018; Song et al., 2019; Chen et al., 2022; Zhou et al., 2024). According to Chen et al. (2022), application of 20 μmol/L $CdCl_2$ to lettuce significantly reduced the chlorophyll (Chl) content in lettuce leaves. It was observed that important enzymes in the synthesis of chlorophyll, such as POR, DVR and HemB are less active under Cd-induced stress, which leads to a decrease in the content of Chl a, b and their total amount. At the same time, the degradation of carotenoids was stimulated and thus their content decreased. The ratio of Chl and carotenoids decreased, while the ratio of Chl a to Chl b increased. In *Oenanthe javanica*, 100 mg Cd/L reduced the content of Chl a and b, while the proportion of carotenoids was very little affected. Chlorophyll b showed greater sensitivity to Cd than Chl a. (Zhou et al., 2024). A significant decrease in Chl a and b content was also found in purslane plants when 100 mg Cd/L was applied (Takabayashi et al., 2011). Cadmium is thought to inhibit the phototransformation of protochlorophyllide to chlorophyll, as well as to promote the enzymatic degradation of chlorophyll by activating chlorophyllase. The possibility of replacing Mg in the chlorophyll molecule with ions of divalent metals Cd, Hg, Zn, Ni, Pb was published by Küpper et al. (1996). Heavy metal porphyrins have been known *in vitro* for a long time. The test results showed that Mg in the chlorophyll molecule was replaced by heavy metals in *in vivo* conditions, which made it impossible for photosynthesis to take place. It has been shown that there is an almost regular relationship between the toxicity of heavy metals and the tendency of their ions to bind in the center of the chlorophyll molecule. The replacement of Mg with heavy metals makes it impossible for the changed chlorophyll molecules to absorb light energy and thus the transfer of electrons is disabled, resulting in the interruption of photosynthesis. Light intensity has a great influence on Mg substitution reactions. In addition to the mentioned elements, Mg in the chlorophyll molecule can also be replaced by some rare earth elements, like La or Ce.

Higher concentrations of Cd affect not only the amount of chlorophyll but also the overall activity of the photosynthetic apparatus and hence, the decrease in the amount of chlorophyll under Cd stress results in a decrease in photosynthesis (Song et al., 2019). According to Dias et al. (2012), 10 and 50 μM Cd in lettuce leads to a significant reduction in the photochemical efficiency of PSII and a reduction of the net CO_2 assimilation rate. Cadmium can reduce or interrupt the photosynthetic electron flow (Voigt and Nagel, 2002; Song et al., 2019). Zhou et al. (2024) also report the influence of Cd stress on photosynthetic electron transport by influencing the amount of active PSII and PSI. Panković et al. (2000) mention that Cd stress affected the ribulose-1,5-bisphosphate regeneration capacity of the Calvin cycle more than other processes. According to Chen et al. (2022), Cd stress inhibited the synthesis of photosynthesis-related proteins or subunits and directly affected the protective mechanism of the photosynthetic system.

Growth responses to cadmium toxicity

In conditions of Cd stress, the reduction of plant growth and mass is closely related to its negative impact on photosynthesis. Even low Cd concentration (1 μM) induced reduction of lettuce growth (Dias et al., 2012). Cadmium exposure leads to significant alterations in plant anatomy. Root cortical cells exhibit wall thickening and increased suberin deposition, limiting Cd transport. In leaves, chloroplasts become swollen with disrupted grana. Mitochondria display condensed matrices and broken cristae. Scanning electron microscopy shows alterations in stomatal density and aperture control. Such changes compromise overall metabolic efficiency (Mushtaq et al., 2025).

Cadmium affected cell division and differentiation. Higher Cd concentrations decreased root dry mass and length while increasing root diameter in tomato (Gratao et al., 2009). In Cd-treated maize seedlings, the fresh root biomass, total root length and primary seminal root length were significantly lower than in the control and had thicker cortex and thicker parenchyma cells (Maksimović et al., 2007; Rahman et al., 2017). Cadmium changes leaf structure in young wheat plants and reduces leaf dry mass, mesophyll thickness, the number and size of vascular bundles and vessel diameter. Thinner chlorenchyma after Cd treatment is possibly due to its negative effect on cell division and elongation (Kovačević et al., 1999). The increases in Cd concentration from 0.5 to 5.0 μM $CdCl_2$ reduced plant height, leaf area, and fresh mass of leaves in young sunflower plants (Panković et al., 2000). In lettuce exposed to 1 and 20 μM Cd, there was a reduction of 16% and 46% of plant dry weight (Dias et al., 2012). Heavy metals and microplastics are almost always found in the soil. Han et al. (2023) have found that the co-existence of Cd and polypropylene-microplastics (PP-MPs) at 50 and 100 μm has a synergistic and antagonistic effect with Cd, depending on the size of PP-MPs. Cadmium accumulation in reproductive tissues leads to pollen sterility, reduced fertilization success, and impaired seed filling. In cereals such as rice and wheat, Cd disrupts assimilate partitioning, resulting in lower grain weight and nutritional quality. High Cd content in grains exceeds food safety thresholds (0.2 mg/kg in rice, WHO/FAO standard), making Cd contamination a global food security issue (Zhou et al., 2022).

According to Monteiro et al. (2012), Cd toxicity induced cyto- and genotoxicity and led to decreased antioxidant capacity in lettuce. The concentration of Cd >1 μM leads to an increase in the presence of hydrogen peroxide, the consequence of which is an increase in the oxidation of proteins and lipids. Silicon can reduce the impact of stress caused by some environmental factors (Lazić et al., 2020). Detoxification of Cd relies heavily on chelation and compartmentalization. Phytochelatins (PCs), short peptides derived from glutathione, bind Cd and facilitate transport into vacuoles. Metallothioneins (MTs) also contribute to binding. Ali et al. (2015) stated that application of salicylic acid can alleviate the toxicity of Cd in oilseed rape. Rahman et al. (2017) demonstrated that exogenous silica can compensate Cd toxicity in field peas. Boron can also alleviate its toxicity by promoting Cd chelation on cell wall components of root cells (Wu et al., 2020). Transport across the tonoplast is mediated by HMA3, ABC-type transporters, and CAX transporters. Vacuolar sequestration prevents Cd from interfering with cytosolic processes and contributes to tolerance in hyperaccumulators such as Thlaspi caerulescens (Yu et al., 2024). According to Amirahmadi et al. (2020), biochar application reduces soil Cd bioavailability and encourages oak seedling growth. Cadmium hyperaccumulator plants have developed a complex mechanism to control the toxic effects of Cd. They form organic complexes with Cd and can thus protect key physiological processes from its harmful impact (He et al., 2017).

CONCLUSION

Soil pollution with heavy metals, including Cd, is a worldwide significant environmental problem. Plants primarily accumulate Cd from the soil, through which it enters the food chain and thus endangers the health of humans and animals. Higher plants can absorb Cd through roots and aerial organs. It is taken up in the form of ions or chelates, where it can interact with ions of other elements. Cadmium is highly mobile in plants in both xylem and phloem. Most of it accumulates in the roots and, to a much lesser extent, in the reproductive organs. Higher concentrations of Cd in plants cause visible, morphological (chlorosis, necrosis, etc.) and invisible physiological and biochemical changes. Phytotoxic concentrations of Cd can already affect the initial phases of plant life and seed germination by inhibiting water uptake and mobilization of seed reserves. The influence of Cd on photosynthesis was studied in the most detail. Cadmium reduces the activity of enzymes important for the synthesis of chlorophyll a and b and promotes their breakdown by activating chlorophyllase, as a result of which their content decreases. Cadmium can replace Mg in the chlorophyll molecule and thus enable photosynthesis to take place. Furthermore, Cd stress leads to a significant reduction in the photochemical efficiency of FSII and assimilation of CO_2 in the Calvin. Cadmium stress leads to a decreased antioxidant capacity in plants. Reduction of photosynthetic productivity and phytohormone activity results in reduction of growth of shoots and roots, reduction of leaf surface and numerous anatomical changes.

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УТИЦАЈ КАДМИЈУМА НА ВИШЕ БИЉКЕ

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РЕЗИМЕ: Кадмијум (Cd) се убраја у тешке метале. Загађење земљишта тешким металима, а тиме и кадмијумом, представља заначајан проблем широм света јер је при већим концентрацијама веома токсичан за живе организме. У ланац исхране кадмијум највећим делом доспева преко биљака. Више биљке могу да усвајају кадмијум преко корена и надземним органима. Највећим делом га усвајају преко корена, из земљишног раствора, због чега оптерећење земљишта кадмијумом преставља велик проблем. Код већине биљака кадмијум се накупља у корену, а у мањој мери у надземним, а посебно у репродуктивним органима. Кадмијум за биљке није токсичан при нижим концентрацијама. Међутим, више концентрације кадмијума код биљака изазивају анатомске, морфолошке, физиолошке и биохемијске промене. Фитотоксичне концентрације кадмијума могу да утичу већ у почетној фази живота биљака: на клијање семена инхибирајући усвајање воде и мобилизацију резервних материја семена, што се неповољно одражава на раст поника. Најдетаљније је проучаван утицај кадмијума на фотосинтезу, што је разумљиво ако се има у виду значај овог процеса у образовању органске материје виших биљака. Његов утицај на фотосинтезу веома је комплексан. Веће концентрације кадмијума смањују садржај хлорофила *а* и *б* и њихов однос, док су каротеноиди мање подложни дејству кадмијума. Кадмијум инхибира фототрансформацију протохлорофилида у хлорофил, а утиче и на његову разградњу активацијом хлорофилазе. Он може да замени магнезијум (Mg) у молекулу хлорофила и да и на тај начин онемогући одвијање фотосинтезе. Кадмијум изазива стрес који значајно смањује фотохемијске ефикасности FSII, утиче на фотосинтетички транспорт електрона, на активност ензима Калвиновог циклуса и тиме на уградњу CO_2 у органска једињења. Смањење фотосинтезе и активности фитохормона има за последицу смањени раст биљака, бројне анатомске и морфолошке промене, хлорозу, некрозу и др. Стога је веома важна заштита животне средине од штетног деловања кадмијума.

КЉУЧНЕ РЕЧИ: акумулација; тешки метал; кадмијум (Cd); дистрибуција; раст; биљке; фотосинтеза; клијање семена; токсичност